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POPULATION DYNAMICS OF BLUE JAYS AT A BIRD FEEDER

MARGARET B. HICKEY[1] AND MARGARET CLARK BRITTINGHAM[2]

ABSTRACT.—Hickey color banded and monitored 2373 Blue Jays (*Cyanocitta cristata*) from 1953 until 1976 at her bird-feeder in Madison, Wisconsin. The mean annual survival rate of Blue Jays calculated from reobservation and recapture data by the Jolly-Seber method was 0.54. The annual survival rates of juvenile and adult jays calculated from band returns by the life table approach were 0.45 and 0.53, respectively. Forty-three Blue Jays lived to be at least seven years old, and the oldest Blue Jay reported was a 14-year-old mated male.

The abundance of Blue Jays fluctuated seasonally and annually. Peak numbers occurred during the breeding season ($\bar{x}$ = 99.0 individuals) after young fledged, and low numbers occurred during the non-breeding season ($\bar{x}$ = 21.3 individuals). The annual abundance of Blue Jays was not correlated with abundance of acorn mast.

Blue Jay populations increased between 1953 and 1976, but changes in numbers were not correlated with local changes in survival rates, rates of reproduction, or changes in migratory behavior. The data are most consistent with the hypothesis that regional changes in survival rates occurred during this time period, and these changes were then reflected in a local increase in the abundance of Blue Jays. *Received 11 Dec. 1990, accepted 9 April 1991.*

Long-term studies of marked individuals are valuable for estimating survival rates and longevity, detecting changes in abundance of bird populations, distinguishing long-term population trends from normal year-to-year fluctuations in numbers, and determining the underlying causes of population fluctuations. The Blue Jay (*Cyanocitta cristata*) is a common species throughout eastern North America, yet relatively little is known about its population dynamics, particularly in comparison to other jays such as the Florida Scrub Jay (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1984). In this paper, we report results of a banding study of Blue Jays conducted from 1953 until 1976 in Madison, Wisconsin. Specifically, we report on survival rates, longevity, and causes of mortality, and we address the following questions: (1) Do Blue Jay populations fluctuate within and between years? (2) Are fluctuations in numbers of Blue Jays correlated with changes in acorn mast abundance? (3) Did the abundance of Blue Jays remain the same during the 23 years of the study? and (4) Can changes in numbers of Blue Jays be correlated with changes in survival rates, reproductive rates or migratory behavior?

[1] Madison, Wisconsin (deceased 1976).
[2] Dept. of Wildlife Ecology, Univ. of Wisconsin, Madison, Wisconsin 53706; Present address: School of Forest Resources, The Pennsylvania State Univ., University Park, Pennsylvania 16802.

TABLE 1
AGE AND SEX OF BLUE JAYS BANDED AT THE HICKEY STUDY SITE, MADISON, WISCONSIN, 1953–1976

Age[a]	Sex		
	Female	Male	Unknown
HY	186	113	943
AHY	154	52	246
UNK	120	55	504
Total	460	220	1693

[a] Hatching year (HY), after hatching year (AHY), unknown (UNK).

METHODS

Study area.—From January 1953 through August 1976, Hickey banded and monitored Blue Jays at her bird feeders. All banding was conducted in the side yard of the Hickey home on the southwest side of Madison, Wisconsin. The yard was approximately 0.2 ha and was on the edge of a mature oak (*Quercus* spp.) and hickory (*Carya* spp.) woodlot about 0.1 km × 1.5 km. The woodlot and surrounding pasture were converted to residential development beginning in the early 1950s and became a mix of lawns, woods, and houses. Between 1953 and 1976, the study area and surrounding residential neighborhood did not change significantly.

Capture and marking.—Blue Jays were captured with funnel traps baited with corn and sunflower seeds and with a platform feeder modified to function as a trap. The traps were opened and baited on a year-round basis whenever an unmarked Blue Jay was observed in the yard. The traps were kept open until all Blue Jays were banded. Most unbanded jays were captured and marked within a day or two of arriving in the yard, and approximately 90% of the Blue Jays frequenting the yard were marked at all times (J. J. Hickey, pers. comm.).

During the 23 years of the study, the only extended period when no marking or sighting occurred was from February–August 1964, when the Hickey family was out of the country. This period has been deleted from the analysis. In other years, there were only occasional months when no data were collected. These months have also been deleted from the analysis. During this study, 2373 Blue Jays were captured a total of 3065 times. Each bird captured was banded with an aluminum U.S. Fish and Wildlife Service band and given a unique combination of color bands. After a number of years, the aluminum bands became thin and worn, so older birds were routinely banded with a new FWS band when they were recaptured. Females captured during the breeding season were sexed by the presence of a brood patch. The sex of all other jays was initially reported as unknown. During the breeding season males were identified when mated to a known female (Table 1).

Determination of age and age ratios.—The ages of Blue Jays captured between 1 June and 31 December were determined by plumage characteristics and color of the mouth lining and recorded as hatching year (HY) or after hatching year (AHY). All jays captured between 1 January and 31 May were recorded as age unknown. For purposes of analysis, each bird was considered to become one year older on 1 June.

For each year, we calculated the ratio of banded juvenile (HY) to adult (AHY) Blue Jays captured or sighted on the study site during the breeding season and fall migration period. Regression analysis was used to test for trends in age ratios during these time periods.

Sightings and band returns.—Sightings of marked birds were recorded daily whenever jays were observed in the Hickey yard. In addition, many of the neighbors also reported sightings of marked birds. A total of 8318 observations of 1599 Blue Jays were reported. Seven hundred seventy-four birds were not observed after the month they were banded. Band returns were used to determine causes of mortality and the migration route.

Population analysis.—The calender year was divided into four seasons corresponding to different periods in the life cycle of the Blue Jay. Divisions into seasons were based on other studies of the Blue Jay and on an examination of the trapping data from this study.

Spring migration was defined as April and May. This is the time period when migrations of Blue Jays have been reported in the Madison area (Schorger 1961, 1964). In this study, the number of new Blue Jays captured rises sharply during April and May, suggesting that new birds are moving through the area (Table 2). At the same time migrants are moving through, many resident birds are nest building and incubating eggs (Bent 1946).

The breeding season was defined as June and July. During this period, some Blue Jays are still incubating eggs, but many others have fledged young (Bent 1946). Post-breeding flocks composed of many family groups are starting to form (Hardy 1961). In this study, fledged young were first captured and banded during June and July (Table 2).

The fall migration period was defined as August and September. The timing and magnitude of fall migration appears to be highly variable. Flocks of migrating Blue Jays have been reported occurring any time from August until the middle of November (Broun 1941, Bent 1946, Middleton 1974). We did not include October and November in the migratory period because few new birds were marked during these months (Table 2). In addition, the majority of banded birds recorded in October were resident throughout the winter.

The remainder of the year (October through March) was defined as the non-breeding season. During this period, stable flocks form that remain loosely associated throughout the winter (Hardy 1961, Racine and Thompson 1983). In our study, few new jays were banded during this period (Table 2).

For each season and year, the total number of jays reported was tallied, and the average number of Blue Jays present per season for all years combined was calculated. Analysis of variance was used to test for differences among means, and a Tukey test ($\alpha = 0.05$) was used to determine which means were different.

The total numbers of jays reported each season and year were tallied and regression analysis was used to test for population trends. For each regression equation, we conducted the Durbin-Watson test for autocorrelation; where the error terms were autocorrelated, the iterative approach was used to transform autocorrelated variables, and the models were re-run (Neter et al. 1985). No models showed autocorrelation after the first iteration.

In order to determine whether the numbers of jays reported at the Hickey study site were representative of population fluctuations occurring in the Madison area, the numbers of jays reported at the Hickey site each December were plotted against the number of Blue Jays reported per party hour on Audubon Christmas Bird Counts in Madison, Wisconsin, during the same years (1953–1975). The correlation coefficient (r) was calculated, and residuals were plotted and examined to ensure that the model was appropriate (Box et al. 1978).

Assessment of mast abundance.—Between 1953 and 1969, the Wisconsin Conservation Dept. (Wisconsin Dept. of Natural Resources) conducted an annual mast and berry production survey. The state was divided into five districts based on geographic location, and acorn production was reported as the percentage of "best conceivable crop" or percentage of full crop. We calculated the Spearman rank correlation coefficients to test whether numbers of Blue Jays present during the non-breeding season were correlated with acorn mast abundance in southern Wisconsin. We also calculated the Spearman rank correlation coefficient between statewide acorn abundance and number of jays present during the fall migration period.

TABLE 2

NUMBER OF FIRST CAPTURES, NUMBER OF INDIVIDUALS, AND SURVIVAL RATES OF BLUE JAYS AT THE HICKEY STUDY SITE REPORTED BY SEASON

Parameters	Spring migration (April–May)	Breeding season (June–July)	Fall migration (Aug.–Sept.)	Non-breeding season (Oct.–Mar.)
Total number of first captures	657	1144	459	113
Total number of first captures HY birds	0	805	419	18
Min–max number of Blue Jays present	7–181	11–300	6–149	2–52
Average number of Blue Jays ± SD (N)	70.2 ± 42.8^{ab} (23)	99.0 ± 71.9^{a} (24)	54.9 ± 34.8^{bc} (23)	21.3 ± 13.2^{c} (24)
Average monthly survival rates ± SD (N)	0.86 ± 0.07^{a} (23)	0.99 ± 0.04^{b} (23)	0.85 ± 0.08^{a} (23)	0.96 ± 0.03^{b} (24)

^{a,b,c} Means within a column sharing a letter are not different ($P > 0.05$).

Determination of survival rates and longevity.—Survival rates were calculated in two ways; from band returns and from sightings and recaptures of marked birds. One hundred eleven of the marked Blue Jays were reported dead. Fifty-one of the 111 band returns were from individuals initially banded within four months of fledging. Band returns from these 51 individuals were used to construct a life table (composite life table dynamic approach) and to calculate juvenile and adult survival rates (Moss et al. 1982).

In addition, seasonal and annual survival rates were calculated using the Jolly-Seber method of estimating survival rates from recapture and sighting data (Jolly 1965, Seber 1965). Survival rates calculated in this manner refer to survival on the study site. The complement of these include both mortality and emigration. Seasonal and annual survival rates were calculated for each year (1953–1976), resulting in 93 seasonal and 22 annual survival rates for Blue Jays on the Hickey study site. In order to compare mean survival rates among seasons of different lengths, monthly survival rates were extrapolated from these seasonal survival rates. Analysis of variance was used to determine whether differences in survival rates occurred among seasons, and a Tukey test ($\alpha = 0.05$) was used to determine which means were different. Regression analysis was used to test for trends in seasonal and annual survival rates between 1953 and 1976.

The longevity of 1599 Blue Jays was calculated from both recapture and sighting data. The 774 individuals that were not seen after the month in which they were banded were omitted from the analysis. For each Blue Jay, we calculated the minimum age (in years) of the bird when last observed. Because many birds were banded as adults, and many individuals were still alive after the last date of the study, these results represent minimum ages. The mean expectation of life (e_x), or average life expectancy, was calculated from the life table (Moss et al. 1982).

RESULTS

Band returns and causes of mortality.—One hundred eleven banded Blue Jays were recovered dead and reported. One hundred eight of the 111 banded Blue Jays which were reported dead were found in Madison, Wisconsin; four were recovered from other areas in Wisconsin, two were recovered in Missouri, and one in Arkansas. Three of the eight migratory individuals were banded as adults, showing that both immatures and adults may migrate.

For 68 Blue Jays (61%) the cause of mortality was unknown. Eleven (10%) were killed by cars; seven (6%) died of disease or injury; five (5%) were intentionally shot; five (5%) were killed by cats; five (5%) died by flying into windows; and 10 (9%) died from miscellaneous causes including drowning, electrocution, being caught in a trap, being caught in a fence or hanged by a string. For the 43 birds where the cause of mortality was reported, 23% were due to what might be called natural causes, 12% were directly due to humans, and 65% were an indirect result of human activities (e.g., cats, windows, cars).

Survival rates and longevity.—The annual survival rates of juvenile and adult Blue Jays as calculated from the band returns were 0.45 and 0.53, respectively (Table 3). The mean annual survival rate ± SD (N = 22) for adults and juveniles combined, calculated by the Jolly-Seber method, was

TABLE 3

COMPOSITE LIFE TABLE FOR 51 BLUE JAYS BANDED DURING HATCHING YEAR[a]

Year	Number alive at start of year (lx)	Number dying in the year (dx)	Annual mortality rate (qx)
0	51	28	0.55
1	23	14	0.61
2	9	1	0.11
3	8	3	0.37
4	5	3	0.60
>4	3	2	0.67

[a] Annual survival rates: hatching year (HY) = 0.45, after hatching year (AHY) = 0.53.

0.54 ± 0.09 (min = 0.38, max = 0.69). The mean monthly survival rates varied significantly among seasons ($F = 32.9$, $P < 0.001$) (Table 2).

Annual survival rates did not show a significant trend between 1953 and 1975 (Fig. 1). There were also no significant trends in within-season survival rates during spring migration ($r = 0.04$, df = 21, $P > 0.5$), the breeding season ($r = 0.04$, df = 21, $P > 0.5$), fall migration ($r = 0.23$, df = 21, $P > 0.05$), or the non-breeding season ($r = 0.39$, df = 22, $P > 0.05$).

The average life expectancy (e_x) for Blue Jays calculated from the life table was 1.4 years. The longevity of Blue Jays calculated from sightings and recaptures of marked birds was as follows: 1105 (69%) Blue Jays were last observed when less than two years old; 43 (3%) of the banded jays lived to be at least seven years old (Fig. 2). Two birds were last seen at a minimum age of 13 years and two jays lived at least 14 years. One of the 14-year-old Blue Jays was banded as an adult male in 1957. He was observed on the Hickey site sporadically between 1957 and 1970. In 1970, at the minimum age of 14, he was mated and feeding young.

Abundance of Blue Jays.—The numbers of Blue Jays reported on the Hickey study site during December were positively correlated with the numbers of Blue Jays reported per party hour on the Madison Christmas Bird Count during the same years (Fig. 3). This positive correlation provides support for the assumption that the number of jays reported by the Hickeys were representative of numbers within the Madison area and not merely a reflection of conditions within one backyard. As a result, fluctuations noted at this site will be interpreted as representative of changes occurring over a larger area.

The average number of Blue Jays present within a season varied significantly among seasons ($F = 11.9$, $P < 0.001$), with peak numbers

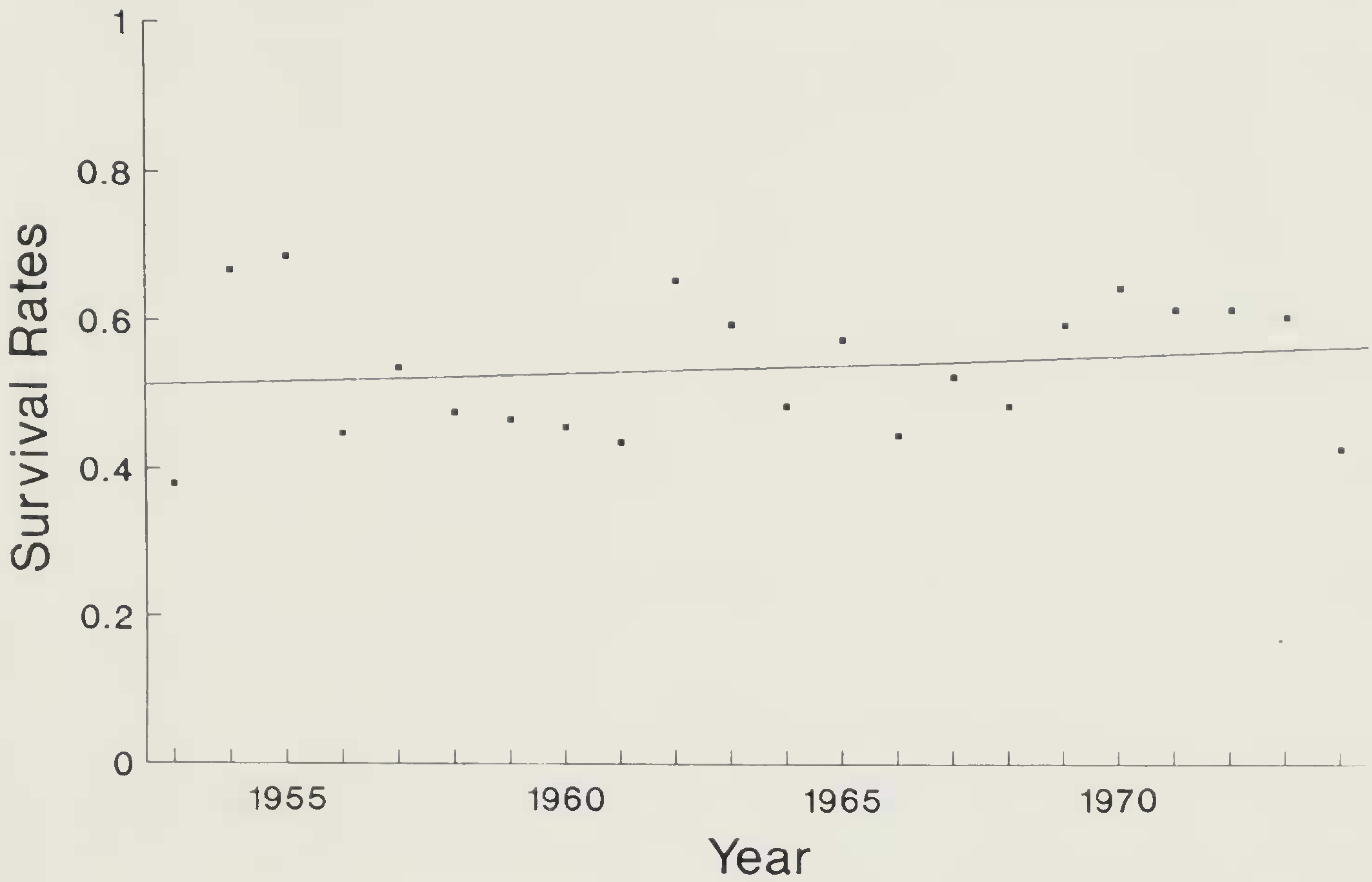

FIG. 1. Annual survival rates of Blue Jays 1953–1975 ($r = 0.18$, df = 20, $P > 0.25$).

occurring during the breeding season and low numbers occurring in the late fall and winter (Table 2).

The total number of Blue Jays present annually on the Hickey site showed a significant increasing trend between 1953 and 1975 (Fig. 4). When the years were broken down into biological seasons, the number

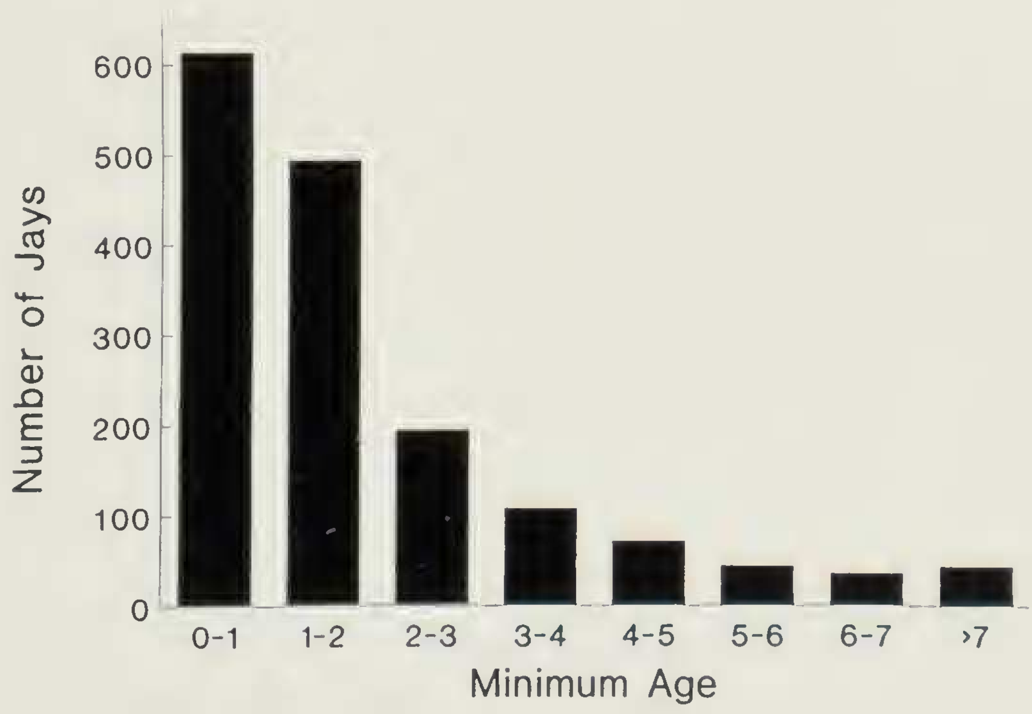

FIG. 2. Numbers of Blue Jays surviving to each age class (N = 1599).

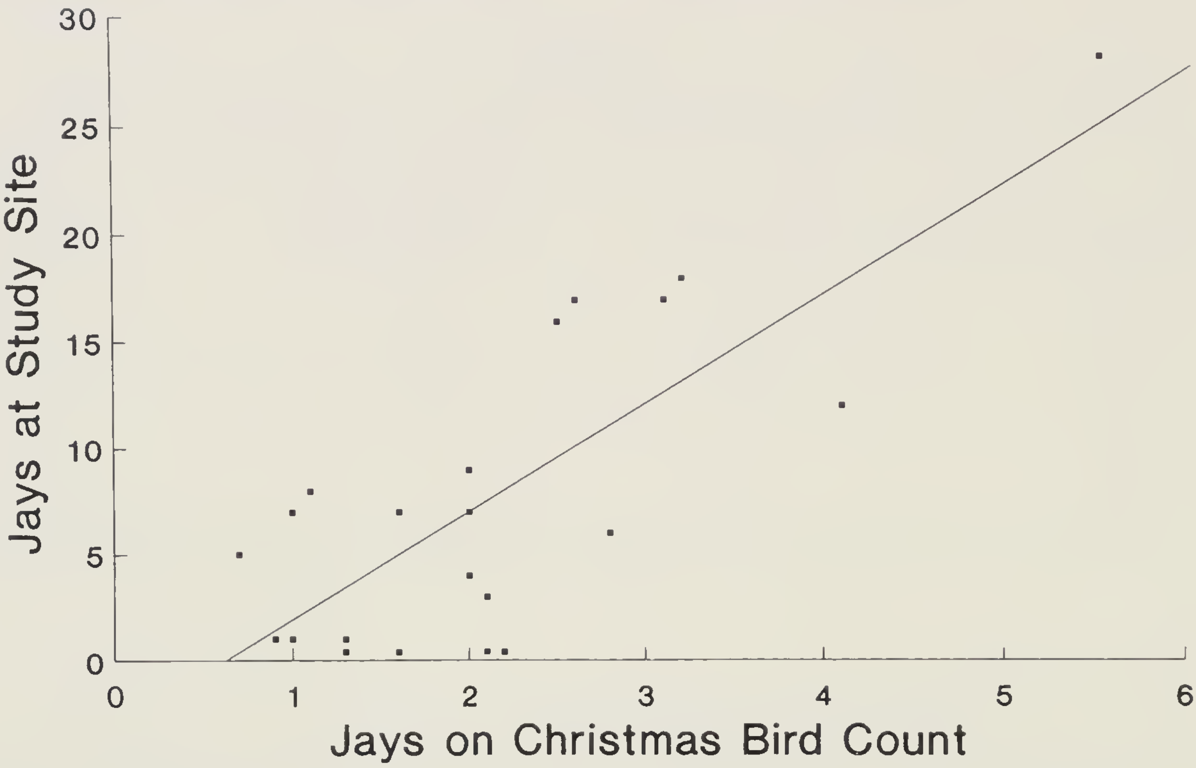

FIG. 3. Number of Blue Jays reported at the Hickey study site each December 1953–1975 and number of Blue Jays reported per party hour on annual Audubon Christmas Bird Counts in Madison, Wisconsin, 1953–1975 ($r = 0.78$, df = 20, $P < 0.001$).

of Blue Jays showed a significant increasing trend between 1953 and 1976 during spring migration ($r = 0.42$, df = 20, $P = 0.05$), the breeding season ($r = 0.57$, df = 21, $P < 0.05$), and fall migration ($r = 0.46$, df = 21, $P < 0.05$). The number of jays present during the non-breeding season showed no significant trend ($r = 0.08$, df = 22, $P > 0.5$).

Number of Blue Jays and mast abundance.—The number of Blue Jays observed during fall migration was not correlated with mast abundance ($r_s = 0.3$, N = 15, $P > 0.25$). The number of Blue Jays present on the Hickey study site during the non-breeding season increased with increasing mast abundance, but the trend was not significant ($r_s = 0.33$, N = 15, $P > 0.10$) (Fig. 5).

Age ratios.—The average ratio ± SD of juvenile to adult Blue Jays reported during the breeding season was 0.51 ± 0.35. The average ratio ± SD of juveniles to adults reported during the fall migration period was 0.53 ± 0.24. The age ratios showed no significant trends between 1953 and 1976 during either the breeding season ($r = 0.11$, df = 21, $P > 0.5$) or during the fall migration period ($r = 0.13$, df = 21, $P > 0.5$).

DISCUSSION

Survival rates, causes of mortality and longevity.—The mean annual survival rate of Blue Jays calculated in this study was similar to rates previously reported for Blue Jays and other passerines (Hickey 1952, Welty 1975, Loery and Nichols 1985). However, annual adult survival

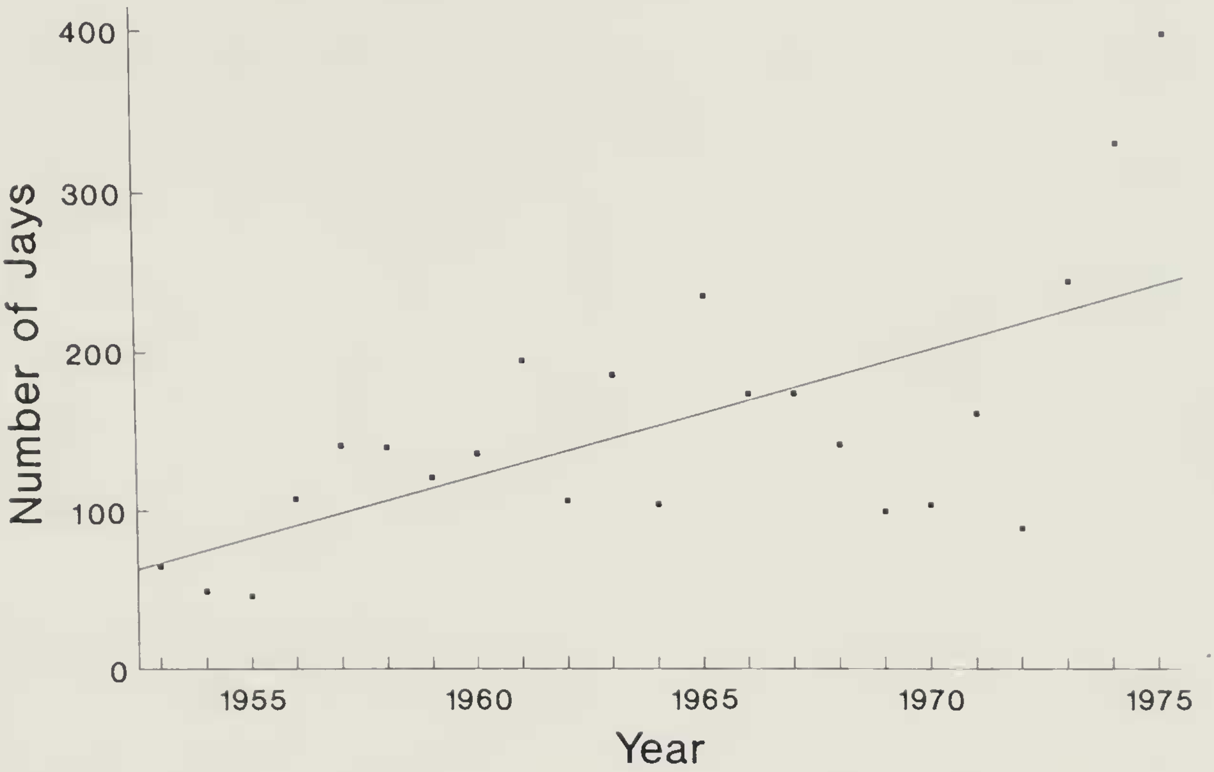

FIG. 4. Total number of Blue Jays reported annually at the Hickey study site 1953–1975 ($r = 0.53$, df = 20, $P < 0.05$).

rates were well below those reported for the cooperatively breeding Florida Scrub Jay ($\bar{x} = 0.82$) (Woolfenden and Fitzpatrick 1984). When broken down into seasons, Blue Jays had higher survival rates during the breeding and non-breeding season than during the two migratory periods, suggesting that seasonal differences in survival estimates are a result of emigration and not higher mortality rates.

The primary causes of mortality for Blue Jays in our study were a result of human activities. However, band recoveries do not provide an unbiased sample of causes of mortality. People are much more likely to find a bird that flies into their window or is brought in by the cat than a bird killed by a hawk or dead from disease. The reported causes of mortality do, however, provide information on the hazards facing songbirds residing in suburban areas.

The oldest Blue Jays reported from five other long-term banding studies were nine years (Bryens 1949, Laskey 1958); 12 years (Harding 1944); and 13 years (Bunting 1944, Beals 1952). The longevity record as reported by the Bird Banding Laboratory is 18 years old (Clapp et al. 1983). The 14-year-old Blue Jay reported in our study is possibly the oldest known breeding Blue Jay.

Seasonal and annual fluctuations in Blue Jay numbers.—Within the year, Blue Jay numbers fluctuated seasonally corresponding with changes in the annual cycle. The lowest number of jays occurred during the winter months. Racine and Thompson (1983) reported winter group sizes varying from 14–49 individuals. The jays in their study were also associated with

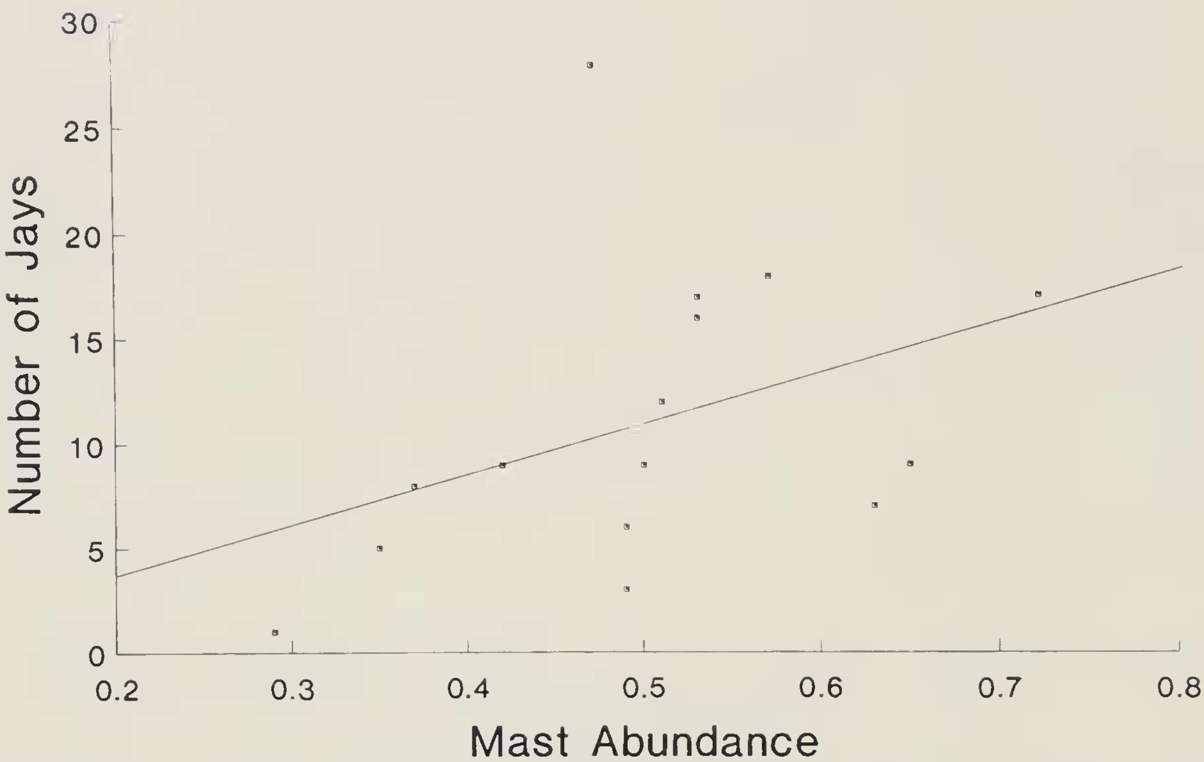

FIG. 5. Abundance of acorn mast in southern Wisconsin (1953–1969) and number of Blue Jays reported at the Hickey study site during the same years ($r_s = 0.33$, N = 15, $P > 0.10$).

a bird feeder. Winter group size in our study showed similar variation. The number of jays increased during the migratory period and peaked in the summer when young Blue Jays entered the population. Numbers declined after fall migration. The abundance of Blue Jays fluctuated among years, but numbers of wintering jays were not correlated with local mast abundance, an important food source for Blue Jays. Smith (1986) attributed variation in wintering Blue Jay numbers in the Ozarks to variation in mast abundance. However, we are not convinced that the data support this conclusion. Out of 369 comparisons made between numbers of jays and mast abundance, 341 resulted in no correlation, seven were negative correlations, and 21 were positive correlations (Smith 1986). Although other researchers have reported mass migrations of Blue Jays out of northern areas in association with low mast abundance (Broun 1941, Nunneley 1964), in our study numbers of migrating jays were not correlated with statewide mast abundance.

Even if Blue Jay numbers do fluctuate with mast abundance, the method of estimating acorn abundance used in our study may be too crude or subjective to detect trends. In addition, Blue Jays in our study were individuals that obtained seed from a bird feeder. Because feeders provide a continuous supply of food, jays which use feeders may be less dependent on acorn mast and less likely to migrate during years of poor mast abundance.

Population trends 1953–1976.—The total number of jays reported annually increased significantly between 1953 and 1976. When each season was examined separately, this trend was noted in all seasons except the non-breeding season. Other researchers using Audubon Christmas Bird Count data, Breeding Bird Census data, and breeding censuses at the same sites over time, have reported increased populations of Blue Jays in both the midwest and northeastern United States during approximately the same time period (Bock and Lepthien 1976, Smith 1986, Wilcove 1988, Terborgh 1989). Increasing populations of Blue Jays have been attributed to an increase in suburban development and the amount of food available at winter bird feeders (Bock and Lepthien 1976, Terborgh 1989). It has been hypothesized that with an increased food supply from bird-feeders, Blue Jays may have higher winter survival rates or may be less likely to migrate in fall (Bock and Lepthien 1976, Terborgh 1989).

If the increased abundance of Blue Jays is a result of winter bird feeders improving winter survival rates, we predict the following: (1) bird feeders are an important source of food to wintering Blue Jays; (2) individuals with access to feeders have higher survival rates than those without access to feeders; and (3) winter survival rates of Blue Jays increased during the years of our study.

If the increased abundance of jays was a result of winter bird feeders changing migratory behavior, we would predict: (1) bird feeders are an important source of food to wintering Blue Jays; (2) the migratory behavior of Blue Jays is flexible enough to respond rapidly to changes in the local food supply; and (3) the number of migrating Blue Jays declined during the years of our study.

Since the physical and nutritional condition of birds can influence the proportion of the population that breeds and the clutch size (Murton and Westwood 1977), a third possibility is that the increase in abundance of jays is a consequence of higher reproductive rates resulting from the increase in food supply provided by bird feeders. Predictions arising from this hypothesis include: (1) bird feeders are an important source of food; (2) all adult Blue Jays do not breed in every year, or the clutch size of Blue Jays is variable; and (3) reproductive rates increased during the years of this study.

All three hypotheses proposed assume that Blue Jays are using bird feeders in the winter and that these feeders provide an important source of food. Brittingham and Temple (1989) surveyed 624 people who feed birds throughout Wisconsin and found that over 90% of them reported Blue Jays regularly visited their feeders during the winter. These results suggests that bird feeders are an important food source to wintering jays.

The survival hypothesis predicts that Blue Jays with access to feeders have higher survival rates then those without access to a supplemental food source. In northern regions, the availability of food in winter is considered to be an important factor influencing survival rates (Lack 1954, 1966). In Wisconsin, Black-capped Chickadees (*Parus atricapillus*) with access to bird feeders have higher survival rates than individuals without access to feeders (Brittingham and Temple 1988). Bird feeders may have a similar effect on Blue Jay survival rates.

The third prediction from the survival hypothesis is that winter survival rates show an increasing trend during our study. We did not detect a change in annual or seasonal survival rates during the 23 years of this study. This does not, however, preclude changes in winter survival rates as a cause of changes in numbers of jays. Our study was conducted at a bird feeder, so any benefit from feeders would have occurred throughout the study, and any banded Blue Jays were feeder users. If bird feeders do increase winter survival rates, survival rates of jays in the Madison area would probably have increased during the years of this study, as the number of people residing in Madison and feeding birds increased. The local increase in survival rates might then result in the increased abundance of Blue Jays detected at the Hickey banding station. In addition, the positive rate of population growth exhibited by the Blue Jay population may have resulted from a change in survival rates occurring prior to the years of this study.

According to the migration hypothesis, Blue Jays have changed their migratory behavior in response to a change in food supply. The Blue Jay is a facultative migrant. During any particular year, the local Blue Jay population consists of both resident and migratory individuals. The subset of individuals that migrate and the causes of migration have been the subject of much debate (Gill 1941, Pitelka 1946, Laskey 1958, Wenger 1975). The most plausible explanation is that the majority of Blue Jays are sedentary but will migrate during years with poor food supplies (Wenger 1975). As a result of this migration strategy, changes in migratory behavior could occur rapidly if changes in the habitat or food supply favored residents over migrants.

A second prediction from the migration hypothesis is that our data show a decline in the numbers of birds banded during the spring and fall migration periods. We did not detect a decline in migrating jays. Instead, between 1953 and 1976 numbers of jays increased during both the migratory periods and remained constant during the winter.

According to the reproduction hypothesis, the increased abundance of Blue Jays resulted from an increase in reproductive rates. In Blue Jays, first year birds typically do not breed (Goodwin 1986). In this study, a few first year birds were observed breeding, but we do not have any information on the proportion of first year birds that bred. We do have data on the proportion of juvenile to adult Blue Jays banded during each year of the study. Although caution should be used in interpreting changes in age ratios (Caughley 1974), if reproductive rates had increased significantly during the years of our study, we would expect to see an increase in the ratio of juveniles to adults banded during the breeding season and fall migration. We did not detect a change in age ratios during either time period, suggesting that a significant change in reproductive rates did not occur.

During the years of our study, the abundance of Blue Jays increased. There is no clear explanation for the observed increase in abundance. The data are most consistent with the hypothesis that regional changes in survival rates occurred either during or prior to the years of this study and that these changes were reflected in larger numbers of Blue Jays.

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